The detection of weakly developed plicidentine in teleost teeth using 3D tomography

by

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Abstract. – The detection of weakly developed plicidentine in ground sections can be difficult, because these structures cannot always be resolved by analysing two-dimensional thin-sections. X-ray tomography followed by 3D virtual modelling allows the non-destructive study of the spatial morphology of these important structures. Here, we illustrate dentine folds in the pulp cavity of the teeth in three teleost fishes, *Arapaima gigas* (Osteoglossiformes), *Hoplias aimara* (Characiformes) and *Lophius piscatorius* (Lophiiformes), and add data from a lepisosteid, *Lepisosteus platostomus*, for comparison. Our observations confirm the presence of plicidentine previously described in these species using ground sections. We also describe for the first time the plicidentine organisation in teeth of the knifefish *Chitala chitala* (Notopteridae), the African electric fish *Hyperopisus bebe* (Mormyriformes) and the Patagonian tooth-fish *Dissostichus eleginoides* (Notothenioidei). We recommend the use of this non-destructive technique in the study of teeth in extant as well as extinct ichthyophagous teleosts, especially when fossil material is too fragile for sectioning.

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Résumé. – Détection de la plicidentine des dents de téléostéens grâce à la tomographie-3D.

La détection de la plicidentine sur des lames minces peut s'avérer délicate quand ce tissu est peu développé. La tomographie X associée à une modélisation 3D est une méthode non destructrice permettant l'étude morphologique spatiale de cette structure. Dans le présent travail, nous montrons des images de plis dentinaires obtenues avec cette technique dans les dents de trois téléostéens, *Arapaima gigas* (Osteoglossiforme), *Hoplias aimara* (Characiforme) et *Lophius piscatorius* (Lophiiforme) et chez le lépisostée, *Lepisosteus platostomus,* pour comparaison. La présence de plicidentine, préalablement observée sur lames minces, chez ces taxons, est confirmée. Nous décrivons également, pour la première fois, de la plicidentine dans les dents du notoptère *Chitala chitala* (Notopteridae), du poisson électrique africain *Hyperopisus bebe* (Mormyriforme) et de la légine de Patagonie *Dissostichus eleginoides* (Notothenioidei). Nous recommandons l'utilisation de cette technique non destructive pour l'étude des dents des téléostéens ichtyophages ainsi que pour le matériel fossilisé tout spécialement quand il est impossible de faire des lames minces lorsque les fossiles sont précieux ou trop fragiles.

Key words
Teleost fish
Lepisosteus
Plicidentine
3D-Tomography

For more than a century and a half, numerous studies have investigated the histological organisation of teleostean teeth (see among others Owen, 1854; Tomes, 1878; Levi, 1939-1940; Lison, 1954; Peyer, 1968). However, despite the high number of valid extant species (more than 31000 according to Froese and Pauly, 2015), descriptive studies of their dental histology have been restricted to only a few hundreds. Currently, we have an incomplete understanding of microstructural diversity of teeth compared to their overall external morphology, which is better documented. The attachment between the tooth and its bone support in particular, has received little attention. Two important papers have, however, been published on this topic (Moy-Thomas, 1934; Fink, 1981), but in our opinion, the histological organization of the dentine at the base of tooth, especially in predatory teleostean fishes, has neither been properly surveyed nor described.

First described by Owen (1841 *in* Tomes, 1878) "plicidentine is a tissue with true dentinal tubules, which is derived from the calcification of a pulp, the odontoblast-carrying surface, of which has been rendered complicated by infolding of its surface". Plicidentine is well known in sarcopterygian fishes and in numerous fossils and extant amniotes (Lison, 1954; Peyer, 1968; Schultze, 1969, 1970; Kearney and Rieppel, 2006; Maxwell *et al*., 2011, 2012; MacDougall *et al*., 2014; Meunier *et al*., 2015a) and has been considered as a feature of this lineage. In contrast, among actinopterygians, plicidentine has only been well known to occur in Lepisosteidae and was considered as almost lacking in the teeth of teleosts. Yet, in his Comparative Odontology treatise, Peyer stated: "Plicidentine […] is well developed in *Lepisosteus* and some other ganoid fishes, but occurs only rarely and then only in very modest development in teleosts" (Peyer, 1968). Unfortunately, he did not provide any example of teleostean

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taxa to illustrate his assertion. Some other authors have also evoked the probable occurrence of plicidentine in the teeth of other teleosts, but without giving any example (Lison, 1954), with the exception of Owen (1854), who reported the occurrence of plicidentine in *Lophius* (in addition to *Holoptychius,* a sarcopterygian), and Thomasset (1930), who mentioned the presence of plicidentine in *Hydrocyon*: "Le genre *Hydrocyon* [= *Oligosarcus* a Characiforme fish] a des dents plissées à la base, sans que cette disposition retentisse sur la structure intime de la dentine".

Plicidentine has been recently described in several predatory teleosts: in the lingual teeth of *Arapaima gigas* (Schinz, 1822) (Meunier *et al*., 2013), in the caniniform teeth of *Hoplias aimara* (Valenciennes, 1847) (Meunier *et al*., 2015a) and in *Lophius piscatorius* Linnaeus, 1758 (Meunier, 2015). However, in these three species, plicidentine is less developed than the highly complex plicidentine found in the teeth of fossil Sarcopterygii (e.g. Bystrow, 1939, 1942, 1950; Schultze, 1969, 1970; Vorobyeva, 1977; Scanlon and Lee, 2002). In actinopterygians, plicidentine is reduced to simple primary folds of the dentine walls of the pulp cavity, and these are localized at the base of the tooth (Meunier *et al*., 2013, 2015a; Meunier, 2015). This explains why the presence of plicidentine in teleost teeth, has repeatedly not retained the attention of morphologists. Fortunately modern 3D-imaging techniques could remedy this difficulty. For example, in the caniniform teeth of the coelacanth *Latimeria*, where plicidentine was previously considered to be absent (Schultze, 1969), recent tomographical studies have allowed the detection of well-developed primary dentine folds in the pulp cavity (Meunier *et al*., 2015b). In all these taxa, plicidentine is interpreted as a specialisation to improve tooth attachment to dental bones in predatory fishes (Meunier, 2014).

The aim of the present paper is to test the efficiency of 3D-modelisation techniques to either confirm or refute the presence of plicidentine around the pulp cavities of teleostean teeth. We have included in this study the teeth of *Lepisosteus plastostomus* Rafinesque, 1802, in which plicidentine is well developed (Peyer, 1968; Schultze, 1969; Grande, 2010), as well as teeth of three teleostean taxa, in which this tissue was previously found, namely: *Arapaima gigas* (Osteoglossiformes), *Hoplias aimara* (Characiformes) and *Lophius piscatorius* (Lophiiformes) (Meunier *et al*., 2013, 2015a; Meunier, 2015). We also tested this technique on the teeth of two closely related Osteoglossomorpha, *Chitala chitala* (Hamilton, 1822) (Notopteridae) and *Hyperopisus bebe* (Lacepède, 1803) (Mormyridae), the teeth of which are smooth, and on another teleostean fish, *Dissostichus eleginoides* Smitt, 1898 (Acanthomorpha: Nototheneidae), whose teeth show axial striae on the external surface suggesting the presence of plicidentine.

MATERIAL AND METHODS

Material

Lepisosteus platostomus Rafinesque, 1820 (Lepisosteidae; Holostei); 630 mm total length (TL). Lower jaw.

Arapaima gigas (Schinz, 1822) (Arapaimatidae; Osteoglossiforme; Teleostei); TL unknown, but lingual tooth-plate is 170 mm long, 35 mm wide. Lingual tooth-plate.

Chitala chitala (Hamilton, 1822) (Notopteridae; Osteoglossiforme; Teleostei); 615 mm (TL). Lower jaw.

Dissostichus eleginoides Smitt, 1898 (Nototheniidae; Perciforme; Teleostei); female specimen, 136, 4 cm TL, 28 kg (Austral Ocean). Premaxilla.

Hoplias aimara (Valenciennes, 1847), (Erythrinidae; Characiforme; Teleostei); a specimen of 15 kg from the Arataye River a tributary of the left side of the Approuague River in French Guyana. Premaxilla.

Hyperopisus bebe (Lacepède, 1803) (Mormyridae; Osteoglossiforme; Teleostei); 280 mm (TL). Lingual tooth-plate.

Lophius piscatorius Linnaeus, 1758 (Lophiidae; Lophiiforme; Teleostei); adult fish (unknown length); MNHN 1932-410. Pterygo-palatine.

Methods

After dissection, the heads were soaked in boiled water to remove flesh, and the bones were air-dried. Lower jaws (*L. platostomus* and *C. chitala*), the lingual bone (*A. gigas*,

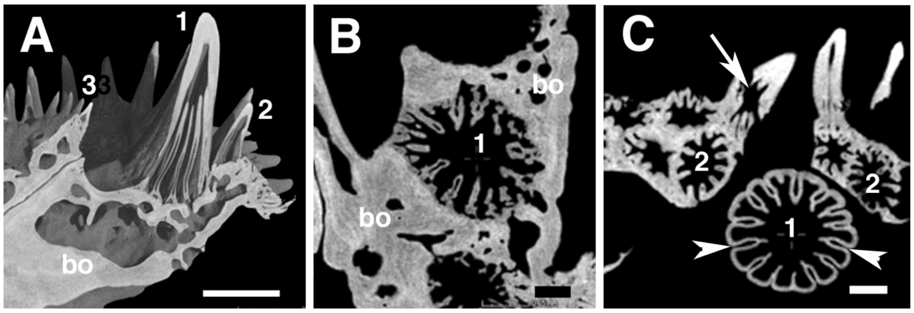

Figure 1. - *Lepisosteus platostomus* (Lepisosteidae). Tomographic imaging of the anterior part of the left lower jaw. **A**: Tridimensional reconstruction of the dentary showing a fang (1), some mid-sized caniniform teeth of the labial side (2), and small teeth on the lingual side (3); **B**: Virtual cross section of the fang (1) near the base of the pulp cavity; the dentine is regularly folded and the folds are fused to the bone of attachment; **C**: Virtual cross section above the precedent one and showing the fang (1) and several mid-sized labial caniniform teeth (2); the dentine is regularly folded in the pulp cavity of the whole teeth. Arrow heads point to external striae of the tooth and the arrow to the plies of an axially sectioned tooth. (bo = bone). Scale bars: A = 2 mm; B, C = 0.5 μm.

H. bebe), and the premaxilla (*H. aimara* and *D. elegenoides*) were disarticulated from the skull.

Non destructive X-ray tomography

The teeth and their supporting bone were X-rayed utilizing a Computed Tomography (CT) imaging system (AST-RX platform and GE Sensing and Inspection Technologies phoenix-ray vltomelx L240-180 CT scanner) at the MNHN,with nanofocus RX source 180kV/15W and detector 400 × 400 mm with a matrix of 2024 pixels (pixel size: 200 × 200 μm). The micro-CT data was processed utilizing *datos|x* reconstruction software (Phoenix|x-ray, release 2.0) and then exported as a 16 bits TIFF image stack. VG studio Max software (Volume Graphics, release 2.2) was used for the analysis and 3D segmentation and virtual reconstruction of the teeth.

The micro-CT scan parameters were:

- *Lepisosteus platostomus* and *Chitala chitala*, voltage 100 kV, current 100 μA, exposure 500 ms, isotropic voxel size 9.45 μm.
- *Hoplias aimara* and *Dissostichus eleginoides*, voltage 90 kV, current 170 μA, exposure: 333 ms, isotropic voxel size 16 μm.
- *Hyperopisus bebe* and *Arapaima gigas*, voltage: 87 kV, current: 130 μA, exposure: 500 ms, isotropic voxel size 9.6 μm.
- *Lophius piscatorius*, voltage: 90 kV, current: 175 μA, exposure: 500 ms, isotropic voxel size 16.8 μm.

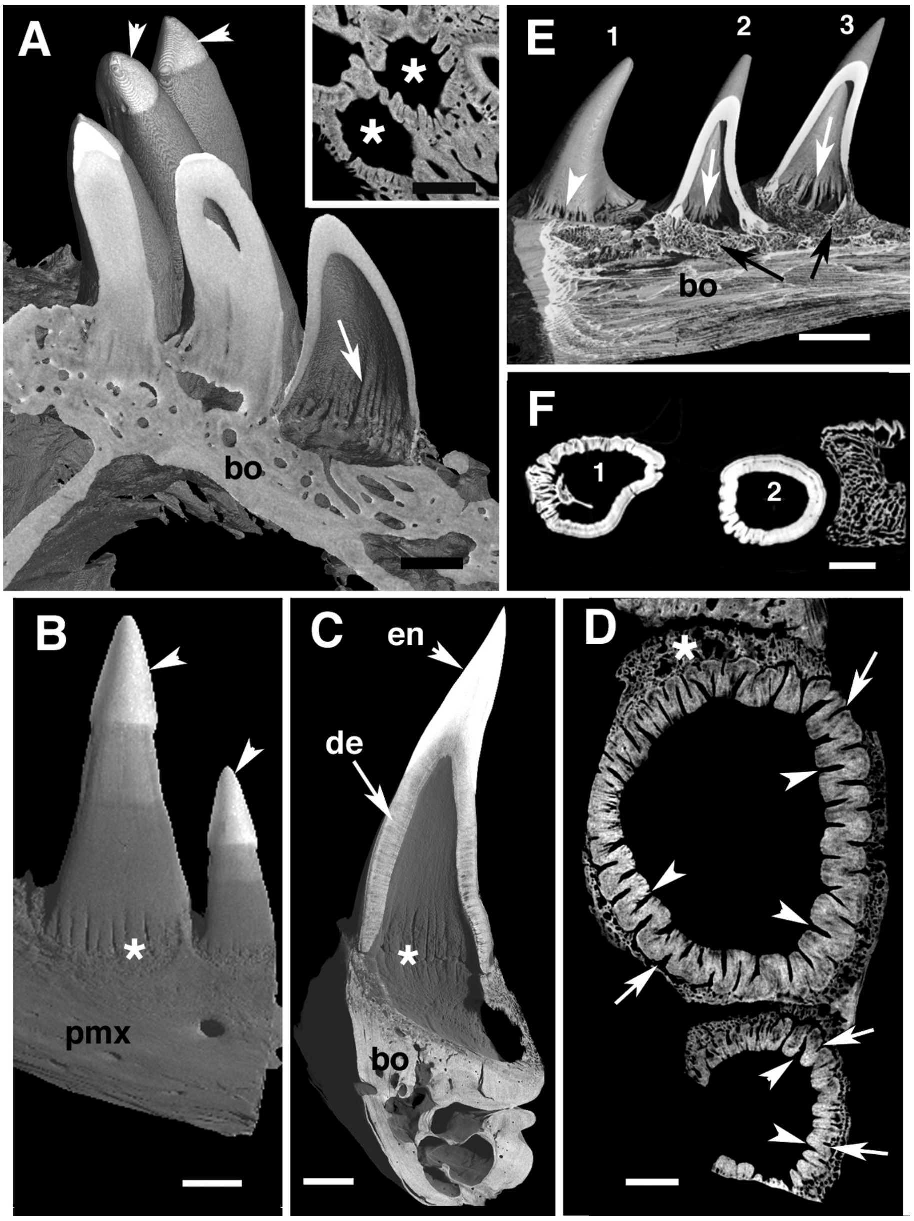

Figure 2. - Tomographic imaging of the teeth of various teleostean taxa known to have plicidentine (see the text). **A**: *Arapaima gigas* (Arapaimatidae). Lingual dentary plate; the axially sectioned tooth (arrow) corresponds to figure 7 *in* Meunier *et al.* (2013); the tooth tip is covered by an enameloid cap (arrowheads); **Inset**: Virtual cross section of the base of several teeth at various levels, a number of which shows dentin folds in the pulp cavity (asterisks). **B-D**: *Hoplias aimara* (Hoplerythrinidae); right premaxilla; **B**: External view of a fang and a mid-sized caniniform tooth showing the basal ridges (asterisk) and the apical enameloid cap (arrow heads); **C**: Virtual axial section of the fang showing the folds in the pulp cavity (asterisk), the apical enameloid cap and the premaxillary bone; **D**: Virtual cross section of the fang (upper) and the mid-sized tooth (lower) showing regular primary folds (arrowheads) and external ridges (arrows); **E-F**: *Lophius piscatorius* (Lophiidae); tomographic image of anterior portion of the left palato-pterygoid; **E**: Basal ridges on the left external surface of a tooth (arrow head); on the right, pulp cavity of two teeth with obvious folds (white arrow). The black arrows point to the attachment bone (bo); **F**: Virtual cross section of the two teeth on the left on Fig. E; the folds are restricted to a part of the teeth. Scale bars: A, D = 1 mm; B, C, F = 2.5 mm; E = 5 mm.

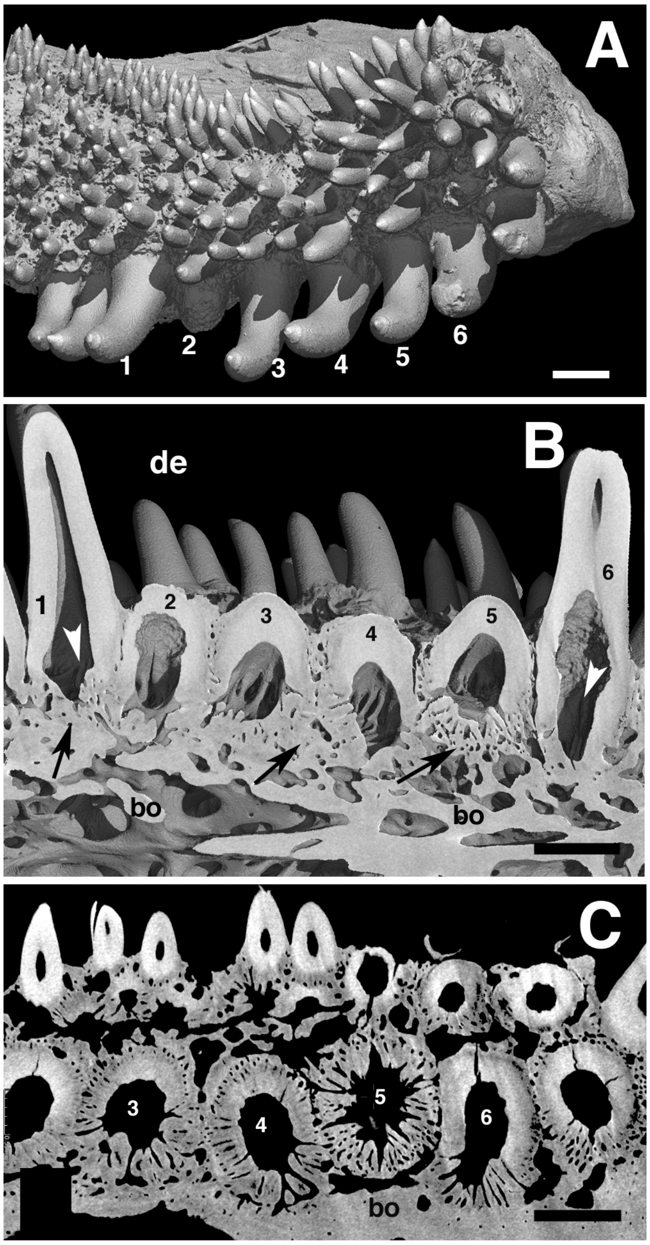

Figure 3. - *Chitala chitala* (Notopteridae). **A**: Tomographic image of the anterior portion of the right dentary; **B**. Virtual longitudinal section of the dentary showing conspicuous folds in the pulp cavity of the four teeth (2 to 5) but also in the neighbouring ones (1, 6; white arrowheads); the teeth are fixed to the supporting bone (bo) by bone of attachment (black arrows); **C**: Virtual cross section of the four labial teeth (3 to 6), showing the pleated dentine. Scale bars = 1 mm.

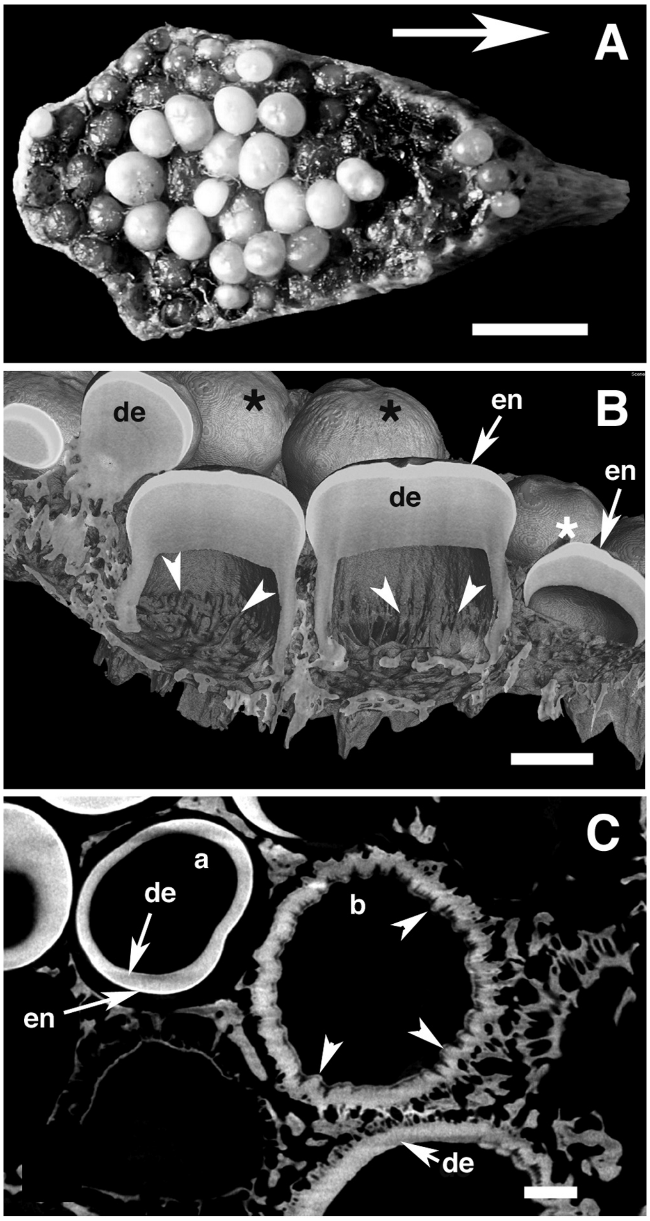

Figure 4. - *Hyperopisus bebe* (Mormyridae); tomographic image of the lingual dentary plate. **A**: Dorsal view of the lingual plate showing a number of side-by-side teeth with roundish apex; white arrow points to anterior; **B**: Virtual model of a part of the lingual plate showing on the foreground two pulp cavities with dentine folds (arrow heads); the teeth are constituted of a dentine core covered by a thick enameloid cap; white and black asterisks point to the roundish apex of teeth (de = dentine; en = enameloid); **C**: Virtual section crossing the pulp cavity of several teeth; the central one (b) shows sharp folds (arrowheads). Section of tooth (a) crosses the higher part of the pulp cavity and the dentine (de) appears as a circular section; it is overlain by a thin enameloid layer (en). Scale bars: A = 2.5 mm; B = 1 mm; C = 0.5 μm.

RESULTS

External tooth morphology

The jaws of *Lepisosteus platostomus*, *Hoplias aimara*, *Chitala chitala*, *Dissostichus eleginoides* and *Lophius piscatorius* present two or three series of teeth depending on their height. The base of the teeth shows obvious axial ridges in *H. aimara*, *D. eleginoides*, and *L. piscatorius,* whereas the external tooth surface of teeth in *Arapaima gigas*, *C. chi-*

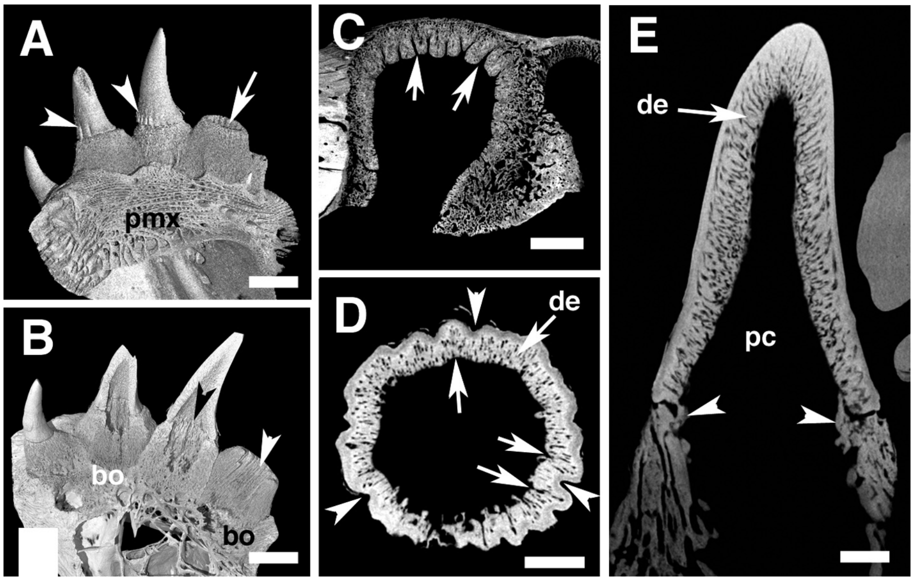

Figure 5. - *Dissostichus eleginoides* (Nototheneidae); tomographic imaging of the anterior portion of the left premaxilla. **A**: Virtual model of the whole premaxilla (pmx) showing the external aspect of three caniniform teeth with external basal ridges (arrowheads); a fourth broken tooth shows ridges in the pulp cavity (white arrow); **B**: Virtual model of the premaxilla (bo) with axial section of the two widest caniniform teeth that show dentine folds in the pulp cavity (black arrowhead); folds are also shown in the broken tooth (white arrowhead); **C**: Virtual cross section in the tooth base at the level of the vascular aperture showing folds in the pulp cavity (white arrows); **D**: Virtual cross section, lightly above the previous level in C, showing dentine folds (white arrows) and external ridges (white arrowheads); the dentine core (de) of the tooth is perforated; **E**: Virtual axial section of the biggest tooth showing thin cavity and canals in the dentine (de); the tooth is covered by a thin enameloid layer; white arrowheads point to folds in the pulp cavity (pc). Scale bars: A, B = 5 mm; C, D = 2 mm; E = 1 mm.

tala and *Hyperopisus bebe* is smooth. In contrast, the teeth of *L. platostomus* show obvious ridges from the base to near the apex.

The tooth crowns selected for this study are either straight (*L. platostomus*, *H. aimara*) or lightly curved (*A. gigas*, *C. chitala*, *L. piscatorius*). A well-developed hypermineralized apical enameloid cap (acrodine) is shown in *A. gigas*, *H. aimara*, *C. chitala* and *D. eleginoides*. The tooth crown is lightly flattened and lancet-like, in *H. aimara*.

The dentary of the shortnose gar, *L. platostomus*, is elongate and bears an inner row of large, widely spaced fangs with external parallel axial ridges that end almost just below the apical cap of enameloid and, an outer row of small, closely spaced teeth morphologically similar to the fangs (Fig. 1). The coronoid elements run along the length of the dentary medially, bearing small teeth. All the teeth of the lingual plate of *A. gigas* have the same length. They are pointed and lightly curved at their summit (Fig. 2A). They do not show any external striation at the tooth base. The jaw of *H. aimara* has caniniform teeth that fall into three groups according to their size (Fig. 1A, B). The tooth base is finely striated, especially on the fangs (Fig. 1C, D). *L. piscatorius* teeth are caniniform and vary in size. They occur on pterygopalatine and dentary bone, and are distributed in the latter into an inner row of large fangs and an outer row of small teeth (see Meunier, 2015 for more details). The pterygopalatine teeth are strongly connected to their supporting bone, contrary to mandibular teeth that are weakly attached. The external side of their base shows parallel, axial ridges that correspond to internal dentine folds (Meunier, 2015) (Fig. 2E, F). The mandibulary teeth of *C. chitala* vary in height, but their external surface is smooth (Fig. 3A). The Patagonian toothfish, *D. eleginoides*, has stout, sharp and caniniform teeth (Fig. 5A). Their apex is curved and their base shows parallel ridges that are crossed by a thin circular ring that corresponds to an unmineralized area of the tooth (Fig. 5A). This circular structure enables tooth breaking and shedding. The teeth of the lingual plate of *H. bebe* are short and wide, with a round apex (Fig. 4A). They are distributed side by side on their supporting bone (Fig. 4A). These teeth are typically molariform.

3D-reconstruction

3D-modelling allowed the virtual visualization of the micro-anatomy of individual teeth, as well as the virtual reconstruction of longitudinal and transverse sections of the various teeth and their associated supporting bones.

All tooth crowns display a pulp cavity and consist of an elongated cone of dentine, generally overlain by an hypermineralized tissue, probably enameloid, the thickness of which varies according to species. Teeth are fixed on their supporting bone by a bone of attachment. Dentine folds are clearly present on the inner wall of the pulp cavity in all specimens studied.

Lepisosteus platostomus

The dentine folds of the fangs are hollow (Fig. 1A, B) and they extend at least to the two thirds of the pulp cavity (Fig. 1A). The smaller teeth also show dentine folds but these folds are not hollow (Fig. 1C).

Arapaima gigas, Hoplias aimara and *Lophius piscatorius*

Dentine folds are clearly noticeable in the basal part of the teeth, but they are limited to 1/3 to 1/2 of tooth height in *A. gigas*, *H. aimara* (Fig. 2A, C) and to the lower 1/3 in *L. piscatorius* fangs (Fig. 2E). On virtual cross sections

(Fig. 2A, D, F), plicidentine folds look similar to the histologic pictures obtained using ground sections (see figs 13, 3A *in* Meunier *et al.*, 2013, 2015a; fig. 3B, C *in* Meunier, 2015).

Chitala chitala

The larger teeth of *C. chitala* present more or less regular dentine folds that are limited to the basal 1/4 of the crown (Fig. 3B). Virtual cross sections show that the teeth are fused to each other at their base through spongy bone (Fig. 3B, C). The supporting bone of the jaw shows numerous medullary cavities. The smaller lingual teeth also show some discrete dentine folds (Fig. 3C).

Hyperopisus bebe

On virtual cross-sections, the apex of some folds looks relatively sharp (Fig. 4C) contrary to the teeth of *A. gigas*, *H. aimara* and *L. piscatorius*, where the tip of folds is relatively rounded (Fig. 2A, D, F). Dentine seems relatively dense, and it is covered by a thick cap of hypermineralized enameloid (Fig. 4B).

Dissostichus eleginoides

Virtual cross sections show that plicidentine is composed of primary folds (Fig. 5C, D) that look like those described in the teeth of *H. aimara* and *L. piscatorius*; these folds are limited to the basal third of the pulp cavity. Externally ridges are apparent on the free surface of the tooth (Fig. 5D). The pulp cavity is perfectly circular in section above the longest folds in the teeth (not illustrated). Dentine shows thin perforations (Fig. 5D) and/or canals (Fig. 5E). This organisation corresponds to a specific variety of dentine named either “vasodentine”, when odontoblastic canaliculi are absent, or “osteodentine” when they are present (see a.o. Lison, 1954; Bradford 1967; Herold, 1970; Schmidt, 1971); however, an histological study on ground sections is necessary to obtain more accurate detail on this dentine tissue, and to check whether odontoblastic processes are present or not.

DISCUSSION AND CONCLUSIONS

Tomography and 3D modelling of the tooth structure in seven extant actinopterygian species clarifies their morphology and confirms the presence of plicidentine in all of them. In these ray-finned taxa, dentine folds are always primary folds. We have coined the term ‘simplexodont plicidentine’ to define this kind of dentine folding (for comprehensive revision see Meunier *et al.*, 2015a).

The seven species studied belong to various teleostean groups whose phylogenetic position differs substantially (Lauder and Liem, 1983; Gardiner and Schaeffer, 1989; Gardiner *et al.*, 2005; Near *et al.*, 2012; Betancur-R. *et al.*, 2013). The presence of plicidentine in their teeth has certainly been acquired independently and thus cannot be considered as retention of a primitive feature with a phylogenetical significance. Six of the taxa (*L. platostomus*, *A. gigas*, *H. aimara*, *C. chitala*, *L. piscatorius* and *D. eleginoides*) are ichthyophagous fishes. Plicidentine greatly increases the attachment surface of the tooth to the basal bone, probably reinforcing the teeth to withstand dental strains during predation. A similar functional adaptation was proposed to explain the structural diversity of plicidentine in the teeth of various Sarcopterygii (Peyer, 1968; Preuschoft *et al.*, 1991; Scanlon and Lee, 2002; Modesto and Reisz, 2008; Maxwell *et al.*, 2011, 2012; Meunier *et al.*, 2015b). Therefore, the presence of plicidentine in the lingual teeth of actinopterygian predatory fishes can also be related to the mechanical constraints endured by the teeth.

In gar-pikes, feeding can be divided in three major phases: the initial strike at the prey, manipulation of the prey following capture and swallowing (Lauder and Norton, 1980). During the two first phases teeth are submitted to high mechanical constraints, which can explain the presence of plicidentine in the teeth of *L. platostomus*. Osteoglossomorph fishes are characterized by having three sets of jaws: a mandibular jaw apparatus anteriorly, a pharyngeal jaw apparatus posteriorly, and between these, two sets a tongue-bite apparatus associated with basihyal and parasphenoid teeth (Sanford and Lauder, 1989, 1990). In these fishes, raking behaviour involves holding the prey firmly in the mandibular jaws (for example in *C. chitala*) while the teeth of the tongue-bite are used during the intraoral crushing and shredding of the prey (for example in *A. gigas*) (Sanford and Lauder, 1990). The basibranchial tooth plate of *A. gigas* assists in the backward movement of prey into the oesophagus (Kershaw, 1976), particularly helped by the teeth with their backward directed tip. These teeth are subjected to mechanical stress requiring a strong anchoring with plicidentine onto the basibranchial bone plate (Meunier *et al.*, 2013). In *H. aimara*, mechanical feeding can be divided in three steps: strike, manipulation and swallowing (Lauder, 1981). During the two first phases, teeth play an important function and are submitted to strong mechanical constraints. To open its mouth for seizing prey, *L. piscatorius* that lives on the bottom staying just on the sediment cannot drop its lower jaws, but instead raises its upper jaws. This increases the volume of the mouth cavity creating an inward current of water that allows engulfing prey; simultaneously, the mandibular hinged teeth swing backward and prey is grasped by the pharyngeal teeth and drawn toward the oesophagus (Field, 1966). To our knowledge, there are no data for the functional anatomy of feeding of *H. bebe* and of *D. eleginoides*. Regarding the former, it seems evident that the molariform teeth of the lingual plate are subjected to strong mechanical constraints that can explain the presence of plicidentine in their teeth. *D. eleginoides* is well known for its ichthyophagous diet, and considering its stout caniniform teeth, the functionality of its jaws probably resembles that of *H. bebe*. Therefore, its seems important that a good attaching of teeth to their supporting bones is necessary.

The observation of plicidentine in histological sections can be difficult when dentine folds are weakly developed and restructured to the base of the pulp cavity in some teleost teeth. This is probably why this spatial organization of the dentine had not retained the attention of scientists. A three-dimensional approach is thus essential to confirm its presence, and 3D-modeling techniques have proven to be effective. Among teleost fishes, plicidentine is probably more ubiquitous than previously thought, at least in predatory fish, as demonstrated in our study. This technique should therefore be more routinely used for studying of teleost teeth, especially for fossil material, which is frequently too scarce and precious to be sectioned.

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REFERENCES

BETANCUR-R. R., BROUGHTON R.E, WILEY E.O. *et al.* [24 authors], 2013. - The tree of life and a new classification of bony fishes. PLOS Currents Tree of Life. 2013 Apr. 18. Edition 1. doi: 10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288.

BRADFORD E.W., 1967. - Microanatomy and histochemistry of dentine. *In*: Structural and Chemical Organization of Teeth (Miles A.E.W., ed.), vol. 2, pp. 3-34. Academic Press Inc.

BYSTROW A.P., 1939. - Zahnstruktur der Crossopterygier. *Acta Zool.*, 20: 283-338.

BYSTROW A.P., 1942. - Deckknochen und Zähn der *Osteolepis* und *Dipterus*. *Acta Zool.*, 23: 263-289.

BYSTROW A.P., 1950. - Microscopic structure of bone and teeth in the carboniferous Crossopterygian *Megalichthys* (Osteolepidae). *Doklady Akad. Nauk,* SSSR, 74(1): 119-121. [in Russian]

FIELD J.G., 1966. - Contributions to the functional morphology of fishes. Part II. The feeding mechanism of the angler-fish, *Lophius piscatorius* Linnaeus. *Zool. Afr.*, 2: 45-67.

FINK W.L., 1981. - Ontogeny and phylogeny of tooth attachment modes in Actinopterygian fishes. *J. Morphol.*, 167: 167-184.

FROESE R. & PAULY D., 2015. - Fishbase: www.fishbase.org. Accessed April 2015.

GARDINER B.G. & SCHAEFFER B., 1989. - Interrelationships of lower actinopterygian fishes. *Zool. J. Linn. Soc.*, 97: 135-187.

GARDINER B.G., SCHAEFFER B. & MASSARIE J.A., 2005. - A review of the lower actinopterygian phylogeny. *Zool. J. Linn. Soc.*, 144: 511-525.

GRANDE L., 2010. - An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 6. Suppl. Issue *Copeia*, 10(2A): 1-871.

HEROLD R.C., 1970. - Vasodentine and mantle dentine in teleost fish teeth. A comparative microradiographic analysis. *Arch. Oral Biol.*, 15: 71-85.

KEARNEY M. & RIEPPEL O., 2006. - An investigation into the occurrence of plicidentine in the teeth of Squamate Reptiles. *Copeia,* 3: 337-350.

KERSHAW D.R., 1976. - A structural and functional interpretation of the cranial anatomy in relation to the feeding of osteoglossoid fishes and a consideration of their phylogeny. *Trans. R. Soc. Lond.*, 33(3): 173-252.

LAUDER G.V., 1981. - Intraspecific functional repertoires in the feeding mechanism of the Characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia*, 1: 154-168.

LAUDER G.V. & LIEM K.F., 1983. - The evolution and interrelationships of the Actinopterygian fishes. *Bull. Mus. Comp. Zool., Harvard*, 150: 95-197.

LAUDER G.V. & NORTON S.F., 1980. - Asymetrical muscle activity during feeding in the gar, *Lepisosteus oculatus*. *J. Exp. Biol.*, 84: 17-32.

LEVI G., 1939-1940. - Études sur le développement des dents chez les téléostéens. 1 – Les dents de substitution chez les genres *Ophidium*, *Trigla*, *Rhombus*, *Belone*. *Arch. Anat. Microsc.*, 35: 101-146. 2 – Développement des dents pourvues de dentine trabéculaire (*Esox*, *Sphyrna*). *Arch. Anat. Microsc.*, 35: 201-221. 3 – Développement des dents de substitution de *Merluccius*, *Chrysophrys*, *Cepola*, *Lophius*. *Arch. Anat. Microsc.*, 35: 415-455.

LISON L., 1954. - Les dents. *In*: Traité de Zoologie (Grassé P.P., éd.). Masson, Paris, 12: 791-853.

MacDOUGALL M.J., LEBLANC A.R.H. & REISZ R.R., 2014. - Plicidentine in the early Permian parareptile *Colobomycter pholeter*, and its phylogenetic and functional significance among coeval members of the clade. *PloS ONE*, 9(5): e96559.

MAXWELL E.E., CALDWELL M. & LAMOUREUX D.O., 2011. - The structure and phylogenetic distribution of amniote plicidentine. *J. Vert. Paleontol.*, 31(3): 553-561.

MAXWELL E.E., CALDWELL M. & LAMOUREUX D.O., 2012. - Tooth histology attachment, and replacement on the ichthyopterygia reviewed in an evolutionary context. *Paläontol. Z*, 86(1): 1-14.

MEUNIER F.J., 2014. - La plicidentine, une adaptation à la prédation chez les Ostéichtyens ? Actes des XV^{e} Journées Tunisiennes des Sciences de la Mer & 3^{e} rencontre Tuniso-française d'Ichtyologie (Madhia, Tunisie, 2013). *Bull. Inst. Natl. Sci. Tech. Mer Salammbô*, N° Spéc. 17: 37-42.

MEUNIER F.J., 2015. - New data on the attachment of teeth in the Angler fish *Lophius piscatorius* (Actinopterygii; Teleostei; Lophiidae). *Cah. Biol. Mar.*, 56(2): 97-104.

MEUNIER F.J., BRITO P.M. & LEAL M.-E.C., 2013. - Quelques données morphologiques et histologiques sur la structure de la plaque dentaire linguale d'*Arapaima gigas* (Osteoglossidae; Teleostei). *Cybium*, 37(4): 263-271.

MEUNIER F.J., DE MAYRINCK D. & BRITO P.M., 2015a. - Presence of plicidentine in the labial teeth of *Hoplias aimara* (Erythrinidae; Ostariophysi; Teleostei). *Acta Zool.,* 96: 174-180.

MEUNIER F.J. MONDÉJAR-FERNÁNDEZ J., GOUSSARD F., CLÉMENT G. & HERBIN M., 2015b. - Presence of plicidentine in the oral teeth of *Latimeria chalumnae* (Sarcopterygii; Actinistia; Coelacanthidae). *J. Struct. Biol.*, 190(1): 31-37.

MODESTO S.P. & REISZ R.R., 2008. - New material of *Colobomyster pholeter*, a small parareptile from the Lower Permian of Oklahoma. *J. Vert. Paleontol.*, 28(3): 677-684.

MOY-THOMAS J.A., 1934. - On the teeth of the larval *Belone vulgaris*, and the attachment of teeth in fishes. *Quart. J. Microsc. Soc.*, 72: 481-498.

NEAR T.J., EYLAN R.I., DORNBURG A., KUHN K.L., MOORE J.A., DAVIS M.P., WAINWRIGHT P.C., FRIEDMANN M. & SMITH W.L., 2012. - Resolution of ray-finned fish phylogeny and timing of diversification. *PNAS*, 109(34): 13698-13703.

OWEN R., 1854. - On the principal forms and structures of the teeth. *In*: The Principal Forms of the Skeleton and of the Teeth (Blanchard & Lea, eds), pp. 229-263. T.K. & P.G. Collins, Philadephia.

PEYER B., 1968. - Osteichthyes. *In*: Comparative Odontology (Zangerl R., ed.), pp. 80-110. Univ. Chicago Press.

PREUSCHOFT H., REIF W.E., LOITSCH C. & TEPE E., 1991. - The function of Labyrinthodont teeth: big teeth in small jaws. *In*: Constructional Morphology and Evolution (Schmidt-Kittler N. & Vogel K., eds), pp. 151-171. Springer-Verlag, Berlin-Heidelberg.

SANFORD C.P. & LAUDER G.V., 1989. - Functional morphology of the "tongue-bite" in the Osteoglossomorph fish *Notopterus*. *J. Morphol.*, 202: 379-408.

SANFORD C.P.J. & LAUDER G.V., 1990. - Kinematics of the tongue-bite apparatus in Osteoglossomorph fishes. *J. Exp. Biol.*, 154: 137-162.

SCANLON J.D. & LEE M.S.Y., 2002. - Varanoid-like dentition in primitive snakes (Madtsoiidae). *J. Herpetol.*, 36: 100-106.

SCHMIDT W.J., 1971. - The normal tooth tissues. *In*: Polarizing Microscopy of Dental Tissues (Schmidt W.J. & Keil A., eds), pp. 51-469. Pergamon Press, Oxford-New York.

SCHULTZE H.-P., 1969. - Die Faltenzähne der Rhipidisiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus* nebst einer Beschreibung der Zahnstruktur von *Onichodus* (Struniiformer Crossopterygier). *Palaeont. Ital.*, New Ser., 35(65): 63-137.

SCHULTZE H.-P., 1970. - Folded teeth and the monophyletic origin of Tetrapodes. *Am. Mus Nov.*, 2408: 1-10.

THOMASSET J.-J., 1930. - Recherches sur les tissus dentaires des poissons fossiles. *Arch. Anat. Microsc.*, 11: 6-153.

TOMES C.S., 1878. - On the structure and development of vascular dentine. *Phil. Trans. R. Soc., Lond.*, 169: 25-47.

VOROBYEVA E.I., 1977. - Evolutionary modifications of the teeth structure in the Paleozoic Crossopterygii. *J. Palaeont. Soc. India*, 20: 16-20.